

Genotype by environment effects and selection for drought tolerance in tropical maize. II. Three-mode pattern analysis

Scott C. Chapman^{1,4,*}, José Crossa¹, Kaye E. Basford² & Pieter M. Kroonenberg³

¹ *International Maize and Wheat Improvement Center (CIMMYT), Lisboa 27, Apartado Postal 6-641, 06600 México D.F., México;* ² *Department of Agriculture, University of Queensland, Brisbane, Queensland 4072, Australia;* ³ *Dept. of Education, Leiden University, Leiden, The Netherlands;* ⁴ *present address: CSIRO Tropical Agriculture, 306 Carmody Rd., St. Lucia, Queensland 4067, Australia; (* author for correspondence)*

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Summary

A selection program in three tropical maize populations aimed to improve tolerance of mid-season to late season drought environments while maintaining grain yield (GY) potential. The selection process employed other attributes that included maintaining a constant anthesis date (AD) and, under drought, shortening the anthesis-silking interval (ASI) and increasing ear number per plant (EPP). Three-mode (genotypes x environments x attributes) pattern analysis, which consists of clustering and ordination, should be able to collectively interpret these changes from ten evaluation trials. Mixture maximum likelihood clustering identified four groups that indicated the populations' performance had changed with selection. Groups containing the advanced cycles of selection were higher yielding in most environments and had lower ASI and higher EPP, particularly in drought environments. Check entries with no selection for drought tolerance remained grouped with the initial cycles of selection. A 3 x 2 x 3 (genotypes by environments by attributes) principal component model explained 70% of the variation. For the first environmental component, ASI was shown to be highly negatively correlated with both GY and EPP while anthesis date (AD) was virtually uncorrelated with other traits. The second environmental component (explaining 10% of the variation) contrasted droughted and well-watered environments and showed that EPP and GY were better indicators of this contrast (in terms of changes in population performance) than were AD or ASI. Three-mode analysis demonstrated that improvements with selection occurred in both droughted and well-watered environments and clearly summarised the overall success of the breeding program.

Abbreviations: ASI – anthesis to silking interval; EPP – ears per plant; G x E – genotype by environment; GY – grain yield

Introduction

In the tropics, annual maize yield losses due to drought are thought to average about 17% but depending on severity and timing of drought can reach 80% (Edmeades et al., 1992). Where drought is consistently late in the season, earlier maturing genotypes may escape its effects. Since the maize crop is particularly sensitive to drought several weeks before and after flowering, attributes such as short anthesis-silking interval (ASI) and a high number of ears per plant

(EPP) can be useful in selection for tolerance to these conditions. These traits are characteristic of superior families under drought, particularly where yields are low and field variation is high (Edmeades et al., 1992).

Through recurrent selection, the CIMMYT Maize Program has developed three late-maturing tropical populations: Tuxpeño Sequía, La Posta Sequía, and Pool 26 Sequía. Selection for tolerance to mid and late season drought was based on a combination of attributes, several of which are highly correlated with grain yield (GY). The objective of this program is to improve

performance under drought conditions while maintaining gains in well-watered environments. Despite the large interaction between these populations and the environment (GxE), significant yield gains have been achieved by simultaneously selecting for ASI and EPP under drought and for yield in both drought and irrigated environments (Bolaños & Edmeades, 1993; Edmeades et al., 1995). A relatively short ASI is an indicator of more rapid early ear growth (Edmeades et al., 1993) and often results in a higher EPP.

Pattern analysis combines methods of classification (e.g. cluster analysis) and ordination (e.g. principal component analysis) and has been used to summarise two-way tables of genotypes evaluated in several environments (genotype x environment array) while studying single attribute response patterns of genotypes across environments (Mungomery et al., 1974; Byth et al., 1976). In Chapman et al. (1996), two-mode analysis of the CIMMYT germplasm showed that: (1) the effects of drought and irrigated environments on genotype discrimination were virtually orthogonal, i.e. that selection in either type of environment alone was unlikely to result in yield gains in both types of environments; (2) the three populations were progressing toward general adaptation to both types of environments. This did not explain how adaptation of the genotypes was affected in terms of the other selection attributes.

Methods of analysing two-way data have recently been extended to study three-way data, i.e., genotype x environment x attribute. Three-mode analyses (mixture cluster analysis and three-mode principal component analysis) have proved to be powerful techniques for studying multi-attribute genotypic responses across environments (Bisford & McLachlan, 1985; McLachlan & Bisford, 1988; Kroonenberg & Bisford, 1989; Bisford et al., 1990; Bisford et al. 1991). These methods cluster genotypes with similar performance patterns across environments and allow study of relationships between these patterns and crop attributes. However, the methods have not been employed to examine selection within populations. In our study of the effectiveness of selection for improved drought tolerance in late-maturing tropical maize populations, our objective was to be able to summarise the interactions of genotypes, environments and attributes and interpret selection-determined changes in response to drought and well-watered conditions.

Materials and methods

Experiments

Fifteen open-pollinated entries were used to represent drought tolerance selection cycles of the elite populations La Posta Sequía (cycles 0, 1, 2, 3), Tuxpeño Sequía (cycles 0, 8 and TS₆ C₁) and Pool 26 Sequía (cycles 1, 2, 3); conventionally selected checks for La Posta (Pop. 43 C₉) and Pool 26 (C₂₃); two intermediate maturity drought tolerant source populations (TL89DTP1 C₅ and DTP2 C₂); and another late maturing check for La Posta and Tuxpeño (TLWD-EL) (Table 1). The three drought-tolerant elite populations have been improved by recurrent selection under irrigation and managed drought conditions (Edmeades et al., 1994; 1996) while the checks are mainly derived from CIMMYT's multi-location population improvement program. Selection indices were used to attempt to hold anthesis date (AD) constant, reduce ASI under drought and increase yields in both drought and irrigated conditions (Edmeades et al., 1995). In La Posta Sequía and Pool 26 Sequía, high EPP under drought was also a selection criterion. La Posta Sequía C₀ was derived directly from Population 43 C₆ while Pool 26 Sequía C₀ was formed from lines of Pool 26 C₂₀ and some insect-resistant lines from early cycles of Pool 26. Hence, these two checks allow a contrast of progress in the drought breeding program with that in the multi-location breeding program (La Posta Sequía C₃ vs Pop. 43 C₉; Pool 26 Sequía C₃ vs Pool 26 C₂₃).

The entries were evaluated in 10 environments in Mexico, including hot and dry selection environments in winter at Tlaltizapán and in summer at Cd. Obregón, and a hot and humid environment in Poza Rica in summer. Environments 1-5 (Table 2) were well-watered in early growth and then irrigation was withdrawn to cause drought stress during flowering and grain filling while environments 6-10 were well-watered throughout. Environment 6 suffered some stress due to iron deficiency at the site despite foliar applications of iron sulphate. Each trial was planted in an alpha (0,1) lattice design (Patterson & Williams, 1976) with three replicates. Details of entries and testing environments are given by Edmeades et al. (1995) and Chapman et al. (1996).

Three-mode analyses for studying genotype x environment x attribute data include a classification method - the mixture maximum likelihood cluster method; and an ordination model - three-mode principal component

Table 1. Genotype code and name, group memberships from 2-mode and 3-mode analysis, and mean values of four attributes (oven-dry grain yield (GY), anthesis date (AD), anthesis-silking interval (ASI) and ears per plant (EPP)) and mode component scores (with adequacy of fit) for 15 entries over 10 environments.

Genotype		Group		AD	ASI	EPP	GY	Component			Proportion of sums of squares explained
Code	Name	2 ^a mode	3 mode	(d)	(d)	(no.)	(t ha ⁻¹)	1	2	3	
1	La Posta Sequía C ₀	1	1	79.1	4.0	0.91	5.07	0.77	-0.07	0.12	0.76
2	La Posta Sequía C ₁	1	1	78.9	3.8	0.95	5.14	0.58	-0.26	0.31	0.59
3	La Posta Sequía C ₂	2	4	77.9	2.4	0.98	5.41	0.08	-0.38	0.13	0.35
4	La Posta Sequía C ₃	2	4	77.9	2.0	1.05	5.43	-0.23	-0.52	0.10	0.66
5	Population 43 C ₉ ^b (La Posta)	1	1	81.4	4.3	0.94	4.87	1.18	-0.22	0.10	0.78
6	Pool 26 Sequía C ₁	3	3	73.8	3.8	0.92	4.87	0.22	0.93	-0.03	0.68
7	Pool 26 Sequía C ₂	3	2	73.7	2.4	1.02	5.20	-0.51	0.29	0.03	0.61
8	Pool 26 Sequía C ₃	3	2	72.3	1.8	1.05	5.34	-0.87	0.27	0.15	0.82
9	Pool 26 C ₂₃ ^b	3	3	77.4	3.8	0.94	5.05	0.53	0.23	0.17	0.64
10	TL89DTP1 C ₅	4	2	72.1	0.8	1.08	5.52	-1.35	-0.08	-0.15	0.88
11	DTP2 C ₅	4	2	72.3	1.9	1.08	5.44	-0.92	0.15	0.26	0.75
12	Tuxpeño Sequía C ₀	1	1	78.5	3.9	0.88	4.63	0.90	0.42	-0.33	0.78
13	Tuxpeño Sequía C ₈	3	4	75.9	1.7	1.02	5.09	-0.26	-0.03	-0.23	0.21
14	TS6 C ₁	4	4	76.4	1.0	1.03	5.44	-0.50	-0.40	-0.21	0.57
15	TLWD-EL ^b	3	1	80.2	3.8	0.96	4.98	0.39	-0.35	-0.42	0.51
LSD (5%)				1.1	1.5	0.07	0.37				

^a Groups in 2-mode identified by hierachial agglomerative clustering of yield (Chapman et al. 1996a)

^b Checks.

Table 2. Environment codes and names, means of four attributes in each of ten environments (for 15 entries) and component 1 and 2 scores (with adequacy of fit). Abbreviations for attributes are as in Table 1.

Environment		AD	ASI	EPP	GY	Component		
Code	Name ^a	(d)	(d)	(no.)	(t ha ⁻¹)	1	2	Proportion of sums of squares explained
1	TL93A I.S.	85.9	8.5	0.60	1.0	0.78	0.34	0.72
2	TL93A S.S.	82.3	4.3	0.85	1.4	0.86	0.31	0.84
3	OB93B S.S.	68.6	4.4	0.90	1.6	0.79	0.11	0.62
4	TL92A I.S.	83.6	2.3	1.00	3.3	0.83	0.23	0.74
5	TL92A S.S.	82.9	2.0	1.05	4.5	0.85	0.22	0.77
6	TL92A W.W.	82.8	2.3	1.05	5.8	0.85	0.09	0.75
7	PR92B W.W.	52.8	-0.1	1.00	6.4	0.58	-0.48	0.57
8	TL93A W.W.	81.8	1.0	1.06	8.3	0.74	-0.29	0.63
9	TL92A W.W.	84.9	1.3	1.20	8.9	0.74	-0.40	0.71
10	TL93B W.W.	58.9	0.4	1.15	10.4	0.65	-0.42	0.60
LSD (5%)		0.9	0.6	0.03	0.2			

^a TL = Tlaltizapán; PR = Poza Rica; OB = Cd. Obregón; 92, 93 = year; A = winter; B =summer; S.S. = severe stress; I.S. = intermediate stress; W.W. = well-watered.

analysis. Lattice adjusted means were used as input for the three-mode analyses.

Mixture maximum likelihood cluster method

This clustering method groups genotypes with similar performance patterns for each attribute across all environments (McLachlan & Basford 1988; Basford & McLachlan 1985; Basford et al., 1990; and Basford et al., 1991). In this method, genotypes are assumed to be a sample from a mixture of various proportions of a specific number of populations (groups). These underlying groups can have different mean vectors and covariance matrices. The parameters of the groups are estimated using the maximum likelihood principle and subsequently each genotype was allocated to one of the underlying groups based on its estimated probabilities of group membership. The approach used an iteration procedure by which an initial grouping of genotypes was specified and the EM algorithm (Dempster et al., 1977) ensures that convergence to a local maximum of the likelihood occurs. In applying the mixture cluster analysis, arbitrary covariance matrices between attributes for each group can be chosen (used here) or a common covariance matrix between attributes for all groups can be chosen (Basford & McLachlan, 1985). The maximum likelihood method of clustering was performed with the FORTRAN program, MIXCLUS3 (an updated version of that listed in McLachlan & Basford, 1988).

The performance pattern for each group obtained by mixture cluster analysis can be displayed in diagrams (performance or response plots) where the estimated mean performance of each group of genotypes for each attribute in each environment is plotted. Such plots describe group \times environment interactions. A lower bound on the standard error of group mean values was calculated by taking the square root of the ratio of group variance for that attribute and the sum of posterior probabilities of belonging to that group (Basford et al., 1994). Multiplying this quantity by 1.5 gave minimum overlap-underlap bars about the mean enabling the groups to be compared (Basford & Tukey, 1997). If bars (which are centred on the means) overlap, then the means are assumed to be not significantly different. Development of statistical tests for this method is ongoing (K.E. Basford, pers. comm. 1996).

Three-mode principal component analysis

This ordination method derives components for each of the three modes (genotypes, environments and attributes) which account for as much as possible of the variation in the data (Kroonenberg & De Leeuw, 1980; Kroonenberg, 1983; 1988). It is not easy to choose an adequate number of components for each mode as these numbers need to be simultaneously determined for all modes. Increasing the number of components complicates the interpretation of results; it is therefore recommended that configuration of components be expressed at as low a dimension as possible (Basford et al., 1990).

The joint plot diagram (Kroonenberg, 1983, pp. 164–165 - a modification of Gabriel's biplot, 1971) was used to depict the component scores of two modes (e.g. genotypes and attributes) associated with a third mode (e.g. environments). In these plots, genotypes are represented by points and attributes by vectors from the origin (the point of average performance). The value of an attribute for a genotype (or a cluster of genotypes) can be determined from projection of a genotype's score on the attribute vector. Genotypes located around the origin of the joint plot are considered to have an average performance for all attributes. Genotypes distributed along the increasing direction of the vector of an attribute have higher than average values for that attribute. Genotypes distributed along the opposite direction of an attribute vector have lower than average values.

The joint plots also display the strength of the associations among attributes. The angle between the vectors of two attributes that are positively correlated is less than 90° . If the attributes are negatively correlated, the angle between their vectors is greater than 90° ; while uncorrelated attributes are orthogonal.

Kroonenberg & Basford (1989) and Basford et al. (1990), suggested that the two-way attribute by site data should be first centered by subtracting the site mean and then standardised by dividing by the standard deviation for each attribute over all sites. In accordance with the procedure followed in our two-mode analysis of these data (Chapman et al., 1996), we centred the data for each attribute, but standardised it by each site rather than over all sites thereby adopting the recommendations of Fox and Rosielle (1982) and Cooper & de Lacy (1994). The three-way principal component analysis was applied to the centred and site-standardised data using the FORTRAN program TUCKALS3 (Kroonenberg, 1994).

Results and discussion

With selection in the three populations, GY and EPP increased, ASI decreased and AD became slightly earlier even though the selection procedure attempted to hold this value constant (Table 1; Edmeades et al., 1995). Environment means for each attribute are presented in Table 2. Well-watered environments (6-10) had higher GY, shorter ASI and a greater EPP than stress environments (1-5). Days to anthesis were earliest in the warmer summer sowings (environments 3, 7 and 10).

Mixture maximum likelihood cluster method

After mixture cluster analysis with four attributes, the group memberships (Table 1) were different to those obtained by hierarchical agglomerative cluster analysis of yield alone (Chapman et al., 1996). They were roughly similar with two groups of drought-tolerant entries and two of check materials, and with 'sub-groups' that differed in maturity. The major difference in group membership was in the distribution of the drought-tolerant entries. Compared with groups clustered on yield (Chapman et al., 1996), in the three-mode clustering the most advanced La Posta Sequía and Tuxpeño Sequía cycles were joined, while the most advanced cycles of Pool 26 Sequía were separated from the original cycles and check (Pool 26 C₂₃).

The performance plots for the groups from the mixture clustering indicate larger group x environment interaction for GY (Figure 1.1), ASI (Figure 1.3) and EPP (Figure 1.4) and relatively less interaction for AD (Figure 1.2). Compared to GY, there was little group rank change for ASI and EPP across environments, particularly low-yielding ones, *i.e.* group 4 entries had the shortest ASI and group 1 the largest for most environments; the situation was reversed for EPP. As Edmeades et al. (1993) demonstrated, a longer ASI is an indicator of relatively slower early ear growth and in severe stress also results in fewer plants having viable ears at harvest.

Attribute values for different groups varied with environment. Group 1 comprised the early generation cycles for La Posta Sequía and Tuxpeño Sequía, the check for La Posta Sequía (Pop. 43 C₉) and a Tuxpeño check (TLWD-EL). This group was the lowest yielding in 4 of the 5 drought environments (Figure 1.1) and no more than average in other environments. The low yields were associated with a high ASI under drought, late maturity and a low EPP (Figure 1). Like group

1, group 3 consisted of entries with little history of drought tolerance breeding: Pool 26 Sequía C₁ and the Pool 26 check (C₂₃). While this group flowered earlier than group 1, the patterns of ASI and EPP were similar resulting in yields that were low to average in drought environments and among the lowest in irrigated environments (Figure 1). Groups 2 and 4 had the lowest ASI and highest EPP in drought environments with resulting higher yields than the other groups (Figure 1). Group 2 consisted of the advanced cycles of Pool 26 Sequía and two populations formed from a diverse array of drought tolerant sources (DTP1 and DTP2). This group was earlier in maturity (Figure 1.2) and lower yielding in the irrigated environments than was group 4. Group 4 was formed of the two most advanced generations from each of Tuxpeño Sequía and another Tuxpeño population, La Posta Sequía.

In general, data for the different covariance matrices for each of the four groups (not shown) indicate small correlations (<0.40) among attributes for all groups. However, high positive correlations (>0.40) between grain yield and number of ears per plant were found for all groups. There were also correlations (>0.37) between AD and ASI in the drought-tolerant groups (2 and 4), consistent with relationships observed elsewhere (Bolaños & Edmeades, 1993). The ASI and EPP were negatively correlated (<-0.30) in all groups except the third. Due to the small number of entries in each group, these correlation results have a low reliability.

Three-mode principal component analysis

The three-mode model with 3 x 2 x 3 components for genotypes, environments and attributes, respectively, was considered adequate for fitting the data ($r^2 = 0.70$), after testing several other combinations of numbers of components for each mode. A 2 x 2 x 2 model accounted for only 63% of the variation and a 3 x 2 x 2 model for 64% while a 3 x 3 x 3 model increased the goodness of fit to only 72%.

In the 3 x 2 x 3 model, the three components for the genotype mode accounted for 52%, 14% and 4% of the variation, respectively; the two components for the environment mode accounted for 60% and 10%, respectively; and the three components for the attributes accounted for 50%, 14% and 6%, respectively. Not all genotypes, environments and attributes were fitted equally well by the model. For genotypes, goodness of fit was low for La Posta Sequía C₂ (0.35) and Tuxpeño Sequía C₈ (0.21), but otherwise ranged from 0.51 to

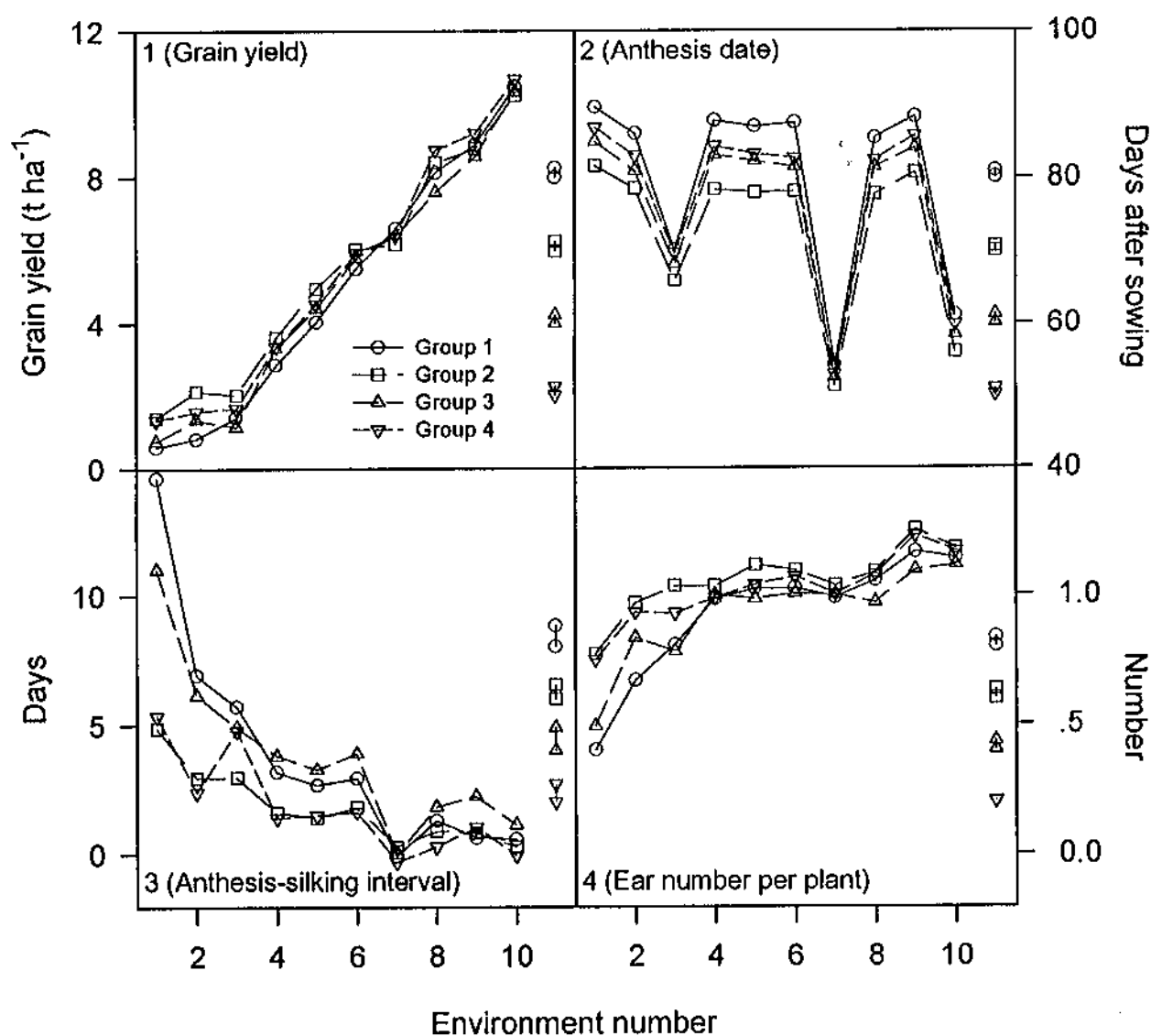


Figure 1. Expected mean of four attributes in each of four groups of entries obtained using mixture cluster analysis. The horizontal axis is the environment rank for mean grain yield. The overlap-underlap bars are the minimum bars for which failure to overlap corresponds to a 'statistical difference' (see text). Figure 1.1–1.4 are the response plots for grain yield, days to anthesis, ASI and number of ears per plant, respectively.

Table 3. Scores and fit for first three components of four attributes over 15 entries and 10 environments.

Attribute	Component			Proportion of sums of squares explained
	1	2	3	
Grain yield (GY)	0.656	0.307	0.320	0.63
Anthesis date (AD)	-0.739	0.622	-0.044	0.93
Anthesis-silking interval (ASI)	-0.709	-0.206	0.351	0.67
Ear number per plant (EPP)	0.722	0.154	0.009	0.55

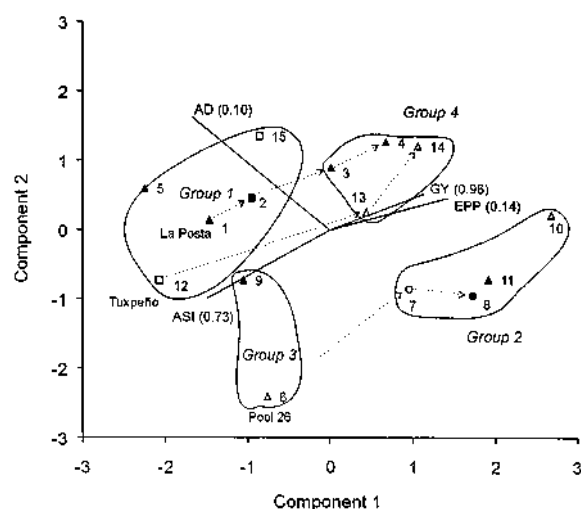


Figure 2. Joint plot of the first two components of 15 entries and four attributes associated with the first environment component. Entries and genotype groups derived by cluster analysis are represented by numbers. These are further coded in the third dimension by symbol type (see text). Vectors (solid lines) for attributes: grain yield (GY), days to anthesis (AD), anthesis-silking interval (ASI) and number of ears per plant (EPP) with numbers in parentheses referring to the score for the third dimension component of each attribute. Dotted arrows represent the progression of selection within three populations.

0.88 (Table 1). A 3 x 3 x 3 model did not improve the fit for these entries. While 93% of the variation in AD was accounted for by the model, other attributes were fitted to a degree ranging from 55 to 67% (Table 3). Environments were generally well fitted by two components with more than 57% of variation accounted for in all environments (Table 2). While the first component did not distinguish among environments (*i.e.* it explained the common pattern over environments), the second component contrasted drought and well-watered environments (Table 2).

1st environment component: Common genotype and attribute patterns over environments

The attributes GY and EPP were highly positively correlated (Figure 2), since their vectors form an angle much smaller than 90°. Both were highly negatively correlated with ASI. The vector for AD was almost at right angles to the other three attributes and is effectively independent of them. Hence, the first attribute component contrasted AD and ASI with GY and EPP, while the second component separated AD and ASI.

For the genotypes, component 1 was associated with improved average performance, especially in

drought environments with the most drought tolerant groups (2 and 4) located to the right in Figure 2. These groups were hence associated with better than average attribute scores for GY and EPP and low values of ASI (Figure 2) as was seen in the performance plots (Figure 1). Genotype component 2 was associated with maturity as the later maturing entries (groups 1 and 4 (see Table 1)) were located toward the top in the plot. These groups generally had higher than average values of AD.

The component 3 scores for the attributes are indicated in parentheses in Figure 2 since the axes would be coming out of the graph toward the reader. Attributes AD and EPP are relatively unimportant for this third component while GY and ASI have high positive scores, *i.e.*. Hence, for two genotypes that had a similar score for components 1 and 2, the entry with the higher score for component 3 had a higher GY, but there would have been little difference between the two genotypes in AD or EPP.

The component 3 scores for the genotypes have been coded by symbols (Figure 2). Open symbols have negative component 3 scores while closed symbols are positive; circles are close to zero, triangles range from 0.3 to 0.7 and squares have absolute scores of greater than 0.7. In two dimensions, the La Posta Sequía and Tuxpeño Sequía entries were apparently similar in yield (*i.e.* relative to the GY vector). The positive component 3 for La Posta Sequía entries, however, increased their yields when projected onto the GY vector compared with the Tuxpeño Sequía entries which had a negative component 3. The Pool 26 cycles began with a slightly negative (open triangle) score for component 3 and improved in terms of GY to end with a positive score. While the groups derived by the mixture method cluster analysis separate genotypes in two dimensions (Figure 2), there is no consistent clustering of similarities within groups in the third dimension. Rather this third component tended to contrast the basic genetic differences of the populations: La Posta Sequía, Pool 26 Sequía and Tuxpeño Sequía.

For the three populations, the progression from left to right (dotted lines) represented increasing GY and EPP with a decreasing ASI. The relatively straight progression from cycle to cycle within each population showed that there was little change with selection in the associations with AD. Both the La Posta Sequía and Tuxpeño Sequía entries 'jumped' from group 1 to group 4 as a result of selection. Similarly, Pool 26 Sequía 'jumped' from group 3 to group 2. Thus, selection has clearly changed the genetic expression

of performance within each population. Using linear regression, Bolaños & Edmeades (1993) were able to demonstrate, for eight cycles of selection in Tuxpeño Sequía, an improvement in yield over both droughted and well-watered environments. Here, using three-mode analysis we similarly showed improved performance over a range of environments for both yield and other selected attributes.

In the same number of cycles that La Posta Sequía was selected for drought tolerance and moved from point (entry number) 1 to 4 on the diagram, the check entry for this population moved from point 1 to 5 (Figure 2). Similarly, the check for Pool 26 Sequía has moved from point 6 to point 9. These checks had been improved in a multi-location system with no specific selection for drought tolerance. Both become later maturing but showed no change in the other traits. Significantly, these checks (5 and 9) were grouped with their respective original cycles (1 and 6), suggesting no change in their performance resulted from selection.

The drought tolerant source populations (entries 10 and 11) were two of the highest yielding entries with high EPP and short ASI. In part, this was because they were also the earliest maturing entries and hence partially escaped the effects of drought.

2nd environment component: Contrast between droughted and well-watered environments

Whereas the first joint plot for environments is three-dimensional, the contrasts between the drought and well-watered environments (negative, except for 6, the environment that endured iron deficiency stress and might also be considered a 'stress' environment) can be described in a single dimension (Figure 3). This figure displays those aspects of the genotype and attribute relationships that are influenced by the differences between drought and irrigated environments on genotypes and attributes, after the effect of average performance (Figure 2) has been removed. The genotypes were contrasted with the La Posta entries and Pool 26 C₂₃ having negative scores while the remainder (apart from TLWD-EL) had positive scores. Drought had a strong effect on GY and EPP, but little effect on AD or ASI (scores close to 0); thus EPP and GY were better indicators of the contrasting effects of the two types of environments. While AD and ASI may have been affected by drought, entries were similarly affected in irrigated and drought environments such that there were no rank changes of entries.

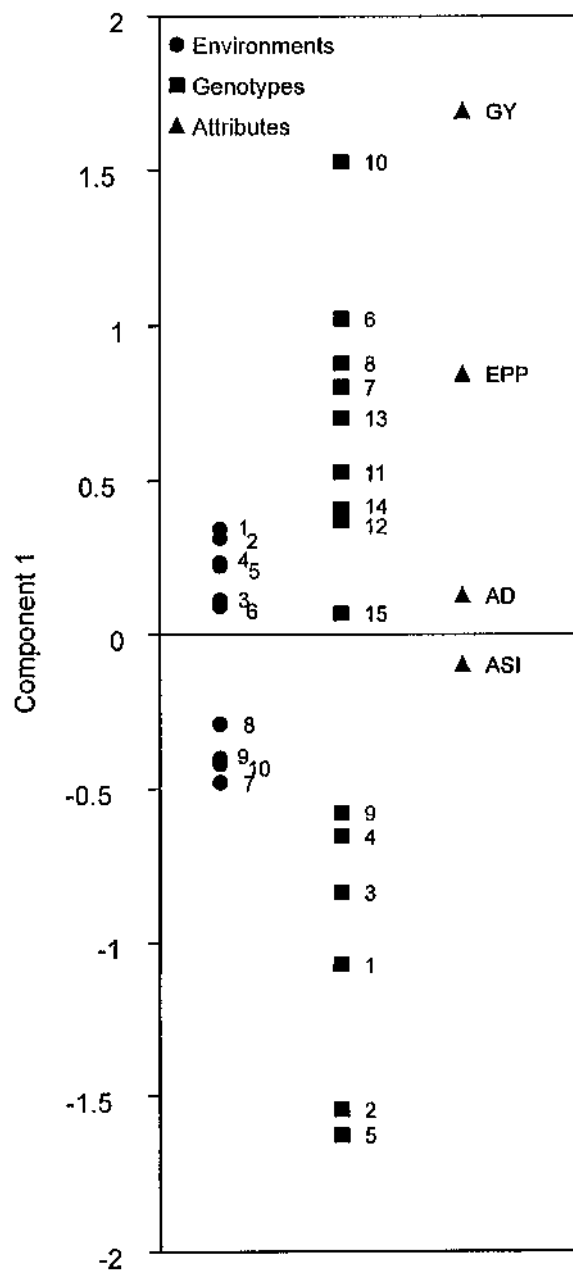


Figure 3. First joint plot component for environments, genotypes and attributes associated with the second environment component.

A product term to compare scores may be calculated as the product of any combination of environment, genotype and attribute scores given in Figure 3., e.g. for the attribute GY, in a drought environment, entry DTP1 (#10, score of 1.5) will have a positive product. For the same attribute and environment, La Posta Sequía C₁ (#2, score of -1.5) would have a negative product of

about the same magnitude. The genotype effect in Figure 3 was likely again to be associated largely with differences in maturity. The later maturing La Posta entries all had negative scores, so that they tend to have relatively lower GY and EPP under drought, but were relatively superior in well-watered environments (positive score combination). The reverse exists for the Pool 26 Sequía (6, 7, 8) and Tuxpeño (12, 13, 14) entries which have positive scores.

While the performance of advanced La Posta Sequía entries (3 and 4) tends to be greater than average over all environments (Figure 2), their yields are relatively depressed in drought environments and relatively enhanced in well-watered environments in contrast to the Pool 26 Sequía and Tuxpeño Sequía entries.

Conclusions

The three-mode analyses have revealed differences in entry performance averaged across environments and contrasts between droughted and irrigated environments. The breeding strategy of simultaneously selecting for shorter ASI and increased EPP in drought environments, and for high GY in both types of environments was shown to result in improvements in performance in all environments. Contrasts in performance between droughted and well-watered environments were related to the general maturity of the populations but also to the improvement for drought tolerance within populations. Recent cycles of selection had high GY and EPP and shorter ASI while initial selection cycles were associated with low GY, EPP and ASI. In terms of classification of performance, these results largely agree with conclusions based on grain yield alone (Chapman et al., 1996). However the advantage of three-mode analysis over two-mode pattern analysis is that classification and ordination were performed using several attributes that had also been part of the selection procedure. Three-mode analyses also described relationships between units not only within modes but also among modes, *e.g.* the effects of ASI in discriminating among genotypes was completely opposite in sign to that of GY or EPP, while the effect of AD, being orthogonal to the other traits, was to separate the maturity effects. The joint plot method of representing performance data has effectively summarised the results of a drought-tolerance breeding program for three late tropical maize populations. The three-mode clustering and ordination methods were able to provide insights into the way the effects of attributes, in

this case traits used in a selection program, combine to improve the adaptation of the three populations to droughted and well-watered environments.

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References

- Basford, K.E. & G.J. McLachlan, 1985. The mixture method of clustering applied to three-way data. *J. of Classification* 2: 109–125.
- Basford, K.E., P.M. Kroonenberg, I.H. DeLacy & P.K. Lawrence, 1990. Multiattribute evaluation of regional cotton variety trials. *Theoret. Appl. Genet.* 79: 225–324.
- Basford, K.E., P.M. Kroonenberg & I.H. DeLacy, 1991. Three-way methods for multiattribute genotype x environment data: an illustrated partial survey. *Field Crop Res.* 27: 131–157.
- Basford, K.E., D.R. Greenway & G.J. McLachlan, 1994. Standard errors of fitted component means of normal mixture models. Centre for Statistics Research Report No. 27. Department of Mathematics, The University of Queensland, Brisbane.
- Basford, K.E. & J.W. Tukey, 1997. Graphical profiles as an aid to understanding plant breeding experiments. *J. of Statistical Inference and Planning* (in press).
- Byth, D.E., R.L. Eisemann & I.H. DeLacy, 1976. Two-way pattern analysis of a large data set to evaluate genotypic adaptation. *Heredity* 37: 215–230.
- Bolaños, J. & G.O. Edmeades, 1993. Eight cycles of selection for drought tolerance in lowland tropical maize. I. Responses in grain yield, biomass, and radiation utilization. *Field Crops Res.* 31: 233–252.
- Chapman, S.C., J. Crossa & G.O. Edmeades, 1996. Genotype by environment effects and selection for drought tolerance in tropical maize. I. Two mode pattern analysis of yield. *Euphytica* 95: 1–9.
- Cooper, M. & I.H. de Lacy, 1994. Relationships among analytical methods used to study genotypic variation and genotype-by-environment interaction in plant breeding multi-environment experiments. *Theoret. Appl. Genet.* 88: 561–572.
- Dempster, A.P., N.M. Laird & D.B. Rubin, 1977. Maximum likelihood from incomplete data via the EM algorithm (with discussion). *J. Royal Stat. Soc. B* 39: 1–38.
- Edmeades, G.O., J. Bolaños & H.R. Lafitte 1992. Progress in breeding for drought tolerance in maize. In D. Wilkinson (Ed.) 'Proceedings of the 47th Annual Corn and Sorghum Industry Research Conference', Chicago, 1992. American Seed Trade Association, Chicago. pp. 93–111.
- Edmeades, G.O., J. Bolaños, M. Hernández & S. Bello, 1993. Causes for silk delay in a lowland tropical maize population. *Crop Sci.* 33: 1029–1035.
- Edmeades, G.O., S.C. Chapman, J. Bolaños, M. Bänziger & H.R. Lafitte, 1995. Recent evaluations of progress in selection for drought tolerance in tropical maize. *Proceedings of the 4th East-*

- ern and Southern African Regional Maize Conference, 28 Mar. – 1 Apr. 1994, Harare, Zimbabwe. CIMMYT, Harare, pp. 94–100.
- Fox, P.N. & A.A. Rosielle, 1982. Reducing the influence of environmental main-effects on pattern analysis of plant breeding environments. *Euphytica* 31: 645–656.
- Gabriel, K.R., 1971. The biplot graphic display of matrices with application to principal component analysis. *Biometrika* 58: 453–467.
- Kroonenberg, P.M. & J. De Leeuw, 1980. Principal components analysis of three-mode data by means of alternating least squares algorithms. *Psychometrika* 45: 69–97.
- Kroonenberg, P.M., 1983. Three-mode principal component analysis. Theory and application. DSWO Press, Leiden.
- Kroonenberg, P.M., 1988. Three-mode analysis. In: S. Kotz and N.L. Johnson (Eds.) *Encyclopedia of Statistics Science*, Vol. 9, pp. 231–236. Wiley, New York.
- Kroonenberg, P.M., 1994. The TUCKLAS line: A suite of programs for three-way analysis. *Computat. Stat. and Data Analysis* 18: 73–96.
- Kroonenberg, P.M. & K.E. Basford, 1989. An investigation of multi-attribute genotype response across environment using three-mode principal component analysis. *Euphytica* 44: 109–123.
- McLachlan, G.J. & K.E. Basford, 1988. *Mixture models: Inference and applications to clustering*. Marcel Dekker, New York, 253 pp.
- Mungomery, V.E., R. Shorter, & D.E. Byth, 1974. Genotype x environment interactions and environmental adaptation. I. Pattern analysis – application to soybean populations. *Aust. J. of Agric. Res.* 25: 69–72.
- Patterson H.D. & E.R. Williams, 1976. A new class of resolvable incomplete block design. *Biometrika* 63: 83–92.